

CONTRIBUTION TO THE THEORY OF THE MOVEMENTS OF DIATOMS.

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THERE are, as is known, two principal hypotheses to explain the enigmatical movements of the cells of Diatomaceæ. The one advanced by Ch. Nägeli seeks their cause in the osmotic currents between the cell and the surrounding water; the other, framed by Max Schulze, supposes that these movements are simply the creeping of the diatoms upon the surface of the object- or cover-glasses, performed by means of a protoplasmic pseudopodium issuing through a slit of the cell membrane. The view of Pfitzer, according to which the cell membrane of these algæ is composed of two distinct halves, one of them being adjusted to the other as a cover upon a box, seemed to give support to Schulze's explanation, and some observers have held that the movement can only take place when the cell is in contact with the glass and in a definite position with relation to it, and that, if that position be changed by shaking the glass with a needle, the movement will cease. Pfitzer himself believes that what is called the rhaphe of many Diatomaceæ is nothing but a slit through which the protoplasmic pseudopodium protrudes. No one has yet been so fortunate as to see the protoplasm passing out through this slit.

To these two old antagonistic hypotheses, each of which has found many apologists and opponents, Otto Müller recently added a new one.¹ After having studied the structure of the cell by means of thin sections,² he comes to the conclusion that the rhaphe is instrumental in transferring protoplasmic currents to the outside of the cell, and acts as a "propeller," by giving to these currents a screw like direction.

¹*Die Ortsbewegungen der Bacillariaceen.* Berichte d. Deutsch. Bot. Gesell. 14: 1896.

²*Die Durchbrechungen der Zellwände, etc.,* *ibid.*, 7: 177. 1889.

These views are opposed (rightly, it seems to me) by Lauterborn,³ who affirms that such an arrangement as supposed by O. Müller could not impart motion to the cell.

I cannot go into the details of all the observations quoted *pro* and *contra* for each of these hypotheses, but if I can trust in my own observations, I am obliged to sustain the theory of osmotic currents. I have been very often in position to observe the movements of these organisms, either incidentally or with purpose, and I have never met with facts which could be advanced against the osmotic hypothesis.

These observations give me the conviction:

1. That the objection that movements are possible only in a definite position of the cell with respect to the glass (which is considered as the substratum) rests upon inexact observations. Many times I have seen cells of Diatomaceæ executing their progressive movements as well in the frontal as in the lateral position.⁴ It is possible that various species behave differently in this line; but in very many of them, and especially in those symmetrical Naviculaceæ and Nitzschieæ, the position of the cell does not influence the movement. It is stopped sometimes by the sudden change of position in consequence of a shock, which may be easily explained by the rigor which generally follows such treatment of the protoplasm.

2. Nor do I think the affirmation exact that contact with the glass is essential to movements.⁵ So far as my own experience reaches, I observed on the contrary that such contact is an impediment to the movement and perhaps is the cause of the transformation of free swimming (gliding) of the cell into creeping. The impediment is found partly in the friction, partly in the sticking of the mucus surrounding the cell membrane to the

³ *Zur Frage nach der Ortsbewegungen der Diatomaceen.* Ber. d. D. Bot. Ges. 12: 73. 1894.

⁴ This observation is in accord with that of O. Müller, that the position towards the substratum does not influence the movement in *Pinnularia*, *Stauroneis Phoenicentron*, and *Nitzschia sigmoidea*.

⁵ The same objection is stated by O. Müller, who observed the movements of the algæ in a drop of water suspended from a cover glass.

glass. It happens sometimes that the movement of translation is stopped for a while, after which the cell seems to make efforts to pluck itself away from the substratum and then runs forward, only to stop again after a little course and to repeat this play again.

And sometimes the cell, stopped in its movement, goes away from the substratum, being retained only by a small gelatinous cushion sticking to the cover glass, and performs small oscillations in that position. It makes the impression that the osmotic currents between the cell and the surrounding water are too weak to overcome the resistance of the adhesive mucus, and cause these oscillations.

Pfitzer, in his interesting study upon Bacillariaceæ in Schenck's *Handbuch der Botanik*, has raised a theoretical objection against the osmotic theory of movements. He suggests that the low velocity of the osmotic current cannot furnish sufficient force to account for the forward motion of the cell. The objection really is based upon a misunderstanding; for in all movements produced by flowing out of liquid from a vessel (or flowing into it) the cause of the movement does not lie in the velocity of the current, but exclusively in the change in the position at the center of inertia, and it is equally true whether the liquid flows out through macroscopical or molecular openings.

We then have no reason to put aside the endosmotic hypothesis of movements, inasmuch as no observation has proved the existence of plasmatic pseudopodia or other organs for creeping;⁶ and, moreover, that hypothesis gives us the basis for the explanation of some peculiarities of these very enigmatic movements.

The movements of the Diatomaceæ were very precisely described by the late E. Borščow,⁷ who discerns three types: first, sliding; second, creeping; third, the above described intermittent movement or leaping.

The most characteristic are the sliding or swimming move-

⁶ O. Müller states in concordance with many further observations that what were considered as flagella are simply alien fungi. "The pseudocilia," says he, "are Abgüsse der Riefenkammern." *Ibid.* 14: 58, 59. 1896.

⁷ Die Süßwasserbacillariaceen des südwestlichen Russland. Kief. 1875.

ments, showing a wonderful periodicity. The cell (usually a symmetric one such as *Nitschia* or *Navicula*) begins to swim with a gradually increasing velocity in some definite direction; then the velocity diminishes, and finally the cell stops its movement to recommence it with the same rhythm in the opposite direction, or in a line differing by some small angle from its first path.

These movements have thus all the characteristics of pendulum movements, *i. e.*, the periodic change of the direction (or of the sine, to speak mathematically), and of the velocity, going through the zero (the stopping of the cell) and attaining its maximum at the middle of the path. These movements, as known, have their origin in such a combination of forces, that the point towards which the acceleration is directed is placed at the middle between the two termini of the movement.

Some observations suggested to me the supposition that this point, in microscopical observation, is determined by the apex of the cone of rays reflected from the mirror to the opening on the stage.

If we consider the osmotic hypothesis as true, to which, as we have seen, there is no serious objection, there are two functions, each of which is most constant in the cell, which may be the source of those products that are the ground of osmotic currents between the cell and its surrounding. These are *respiration*, which is continuous and the products of which are perpetually exosmosed by the cell, and *assimilation*, which takes place only in light, and which produces most probably some kind of sugar (as is known, the *Diatomaceæ* do not contain starch), that is, a substance of high osmotic activity and producing osmotic attractions to the interior of the cell.⁸

Many times I have observed that the movements of the *Diatomaceæ* are very energetic when freshly collected and brought under the microscope in the fresh, cold water, espe-

⁸The osmotic tension in the cells of *Pinnularia major* and *Surirella biseriata* as measured by plasmolysis is no less than 4 or 5 atmospheres (*Cf.* O. Müller, *ibid* 7: 169, 1889). That shows how strong must be the predominance of endosmosis over exosmosis.

cially when it is spring water. Gradually, during the time of the observation, the movements became less active, and at the end—if the drop is not changed—they cease altogether. That is quite explicable by the contained gases in fresh and cold water, which are gradually exhausted or evaporated, in consequence of the warming of the drop. This observation gives equal support to both of the functions proposed as causal.

But there are some other observations which seem decisive in favor of the assimilation being the real cause of movements. These are:

1. *The dependence of movements upon light.*—It is impossible to make direct observation in darkness, as in these conditions we could see nothing; but the following experiment speaks for the above stated dependence: If, while observing a cell in movement, we suddenly cover the mirror so as to intercept all the rays of light, upon uncovering of the mirror after some minutes we generally find the cell at rest not far from the place where it was seen before the light was cut off. It does not start forward at the moment when light is again admitted, but for some time seems to be in a state of rigor and then gradually begins to move. That little experiment was repeated many times, and always with success.

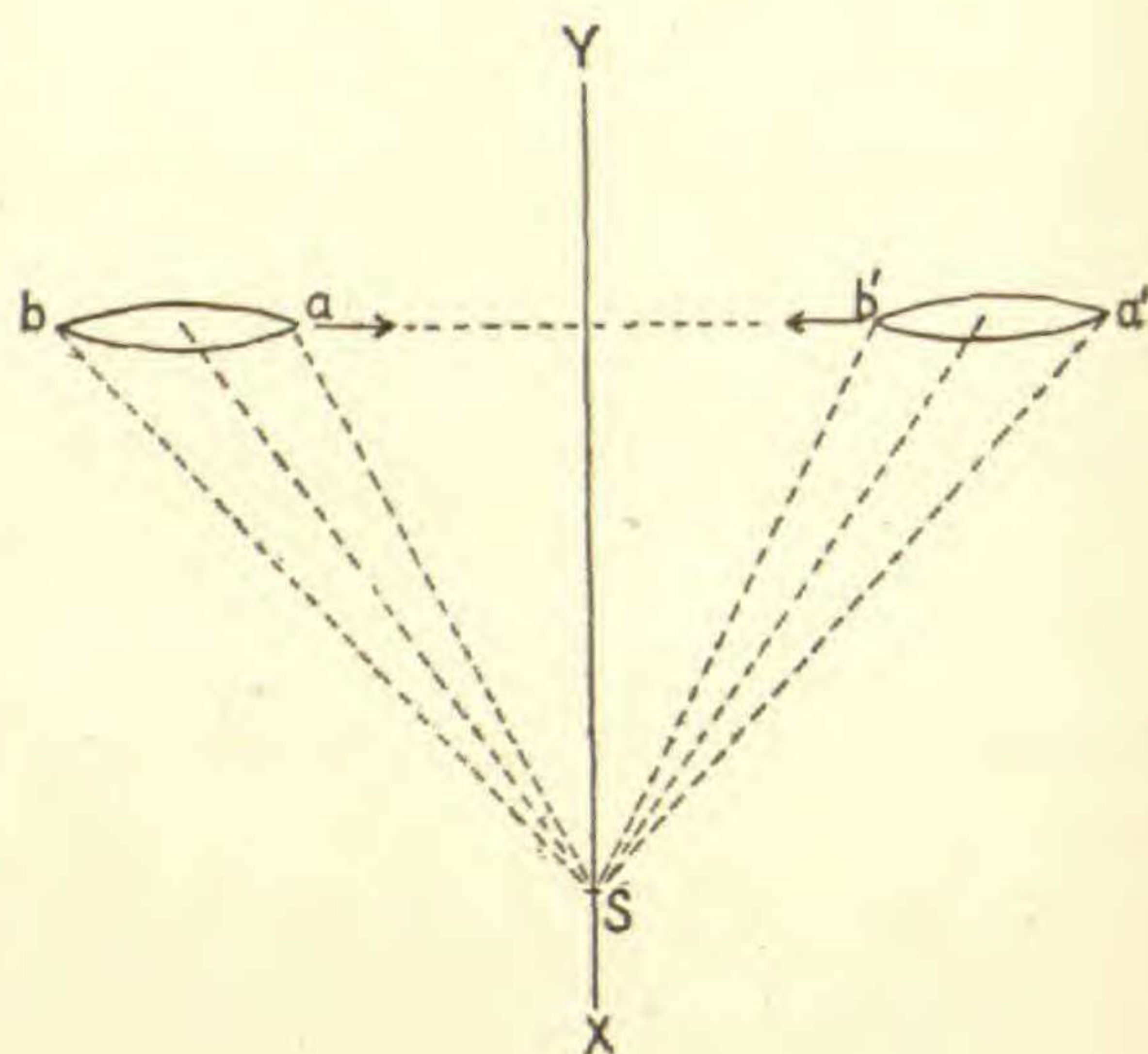
2. *The dependence of the movement upon the color of the light.*—I used for this purpose the light transmitted through solutions of ammoniated copper oxide and of bichromate of potassium, both 1^{cm} thick. As shown by spectroscopic analysis the first allowed the more refrangible rays from the middle of green to pass; the second transmitted the opposite part of the spectrum. The blue rays do not promote the motion; the red ones promote them very energetically. By means of such rays I succeeded in setting in movement some big cells of *Pinnularia*, *Surirella*, and others, quite immobile in the daylight.

3. *The dependence of movements upon the direction of light.*—If we remove slowly the slide carrying a diatom moving in the manner described, so as not to allow the cell to cross a plane passing through the apex of the light cone perpendicular to the

path of the cell, *i. e.*, so that the light should fall always ahead of the cell, we can arbitrarily prolong the movement in the same direction and hinder the cell from retracing its path.

These observations showing the dependence of movements upon light, their prevalence in the red light which, as known, is the most advantageous for assimilation, and the influence of the direction of incident light on that of the movements, give support to the supposition that assimilation is the real ground of movements.

That being stated, how shall we conceive the mechanism of these movements? Imagine a diatom cell to be at a certain distance from the apex (*s*) of the light-cone, with one of its ends directed toward it (see figure).



The half directed towards the light (which we will name the anterior) will receive more light (because of the less inclosed direction of rays towards it) than the posterior half. Consequently assimilation will take place here with more energy, and in the same ratio the endosmotic current to the interior of the cell will be more energetic, since it is dependent on the quantity of elaborated products of assimilation. The result will be that the cell will be impelled towards the source as a canoe would be in whose bow a suction pump had been placed.

While the cell is approaching the apex of the light-cone, the difference of insolation of both halves of the cell is gradually lessened, and thus the acceleration in the given direction, depending upon this difference, grows more and more near zero, which value it reaches at the moment when the center of the cell corresponds to the plane (*xy*) passing through the apex of the light-cone perpendicular to the direction of the movement at the cell.

At this point its velocity attains its maximum because of the sum of all the foregoing accelerations.

After this plane is crossed the conditions are changed; the posterior end receives now more light than the anterior; the process of assimilation is going on there with more energy, and as the result the osmotic currents to the interior of the cell are strengthened. The direction of the acceleration (always being toward the center of light) is inverted as to the direction of the movement, which it now impedes. The velocity is thus gradually lessened, and after having reached zero is changed, too. The cell now runs back, repeating the same type of movement as it did when going forward, and those oscillations are repeated many times.

They would go on in the same plane, were they not disturbed by some occasional hindrance, such as the currents produced in water by heat, contact with other bodies, and so on, which effect a deviation from the primary direction and a return at some angle to it.

If we take into consideration the very low velocity of the diatom cells and their small mass, the slight difference in the quantity of light received by the two halves of the cell will not appear insufficient to account for its movement.

It is not impossible that other kinds of movement could be reduced to this gliding type and be explained in the same way. The above described observations make it not improbable that these other kinds can be deduced from the first one by the action of some hindrance, such as the sticking of the mucus surrounding the outside of the cell to the glass, or the friction when the cell is approaching one of the glasses.

The explanation here proposed, making the periodicity of the movements dependent upon the artificial disposition of the light in the microscope, which is hardly to be found in nature, does not indeed exclude motion under natural conditions. For the matter is not essentially changed by the fact that the rays, instead of being divergent, are parallel, and that their direction towards the cell is unchanged by its movement, as is the

case in daylight. The result will be a movement towards light, or as it is generally termed positive phototaxis. That such a phenomenon really exists among the Diatomaceæ everyone knows who has observed the pools containing these algæ in a summer day. And this kind of phototaxis, which the Diatomaceæ have in common with the great part of unicellular organisms containing chlorophyll, is without doubt of use to them, for moving towards the light places the cells in the most advantageous conditions for assimilation.

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